

# SILICIFIED TRILOBITES OF THE FAMILY ASAPHIDAE FROM THE MIDDLE ORDOVICIAN OF VIRGINIA

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ABSTRACT. Protaspis, meraspis, and holaspis stages of *Isotelus giselae* sp. nov. from the Edinburg Formation (Middle Ordovician) of Virginia are described; diagnostic features of the dorsal shield are the absence of a distinct lateral depression, and the short, strongly elevated palpebral lobes. Four moults during the protaspis period are defined by changes in the hypostomes. *Isotelus* spp. A-E, from the lower and upper Lincolnshire, Oranda, and Martinsburg Formations (Middle Ordovician) of Virginia are based on less complete material. *Nahannia* sp. is described from the Lincolnshire Formation.

THE first description of silicified meraspis and holaspis *Isotelus* material from the Martinsburg Formation of Virginia was provided by Whittington (1941). Evitt (1961) gave a detailed account of the protaspis ontogeny of *Isotelus*, based on material from the lower Lincolnshire, Edinburg, and Martinsburg Formations. Hu (1975) described *Isotelus* protaspides (as *Remopleurides*), meraspides, and holaspides from the Edinburg Formation. In this paper, six species of *Isotelus* and one of *Nahannia* are described from five Middle Ordovician horizons near Strasburg, Virginia (Table 1), with emphasis on the distinction between generic and specific developmental characters. The differences between the species are greatest at the protaspis stage. Mode of occurrence, preservation, and techniques employed are as described by Whittington and Evitt (1954, p. 5). Localities are as described by Whittington (1959, p. 380) and Evitt (1953, p. 34; 1961, p. 987).

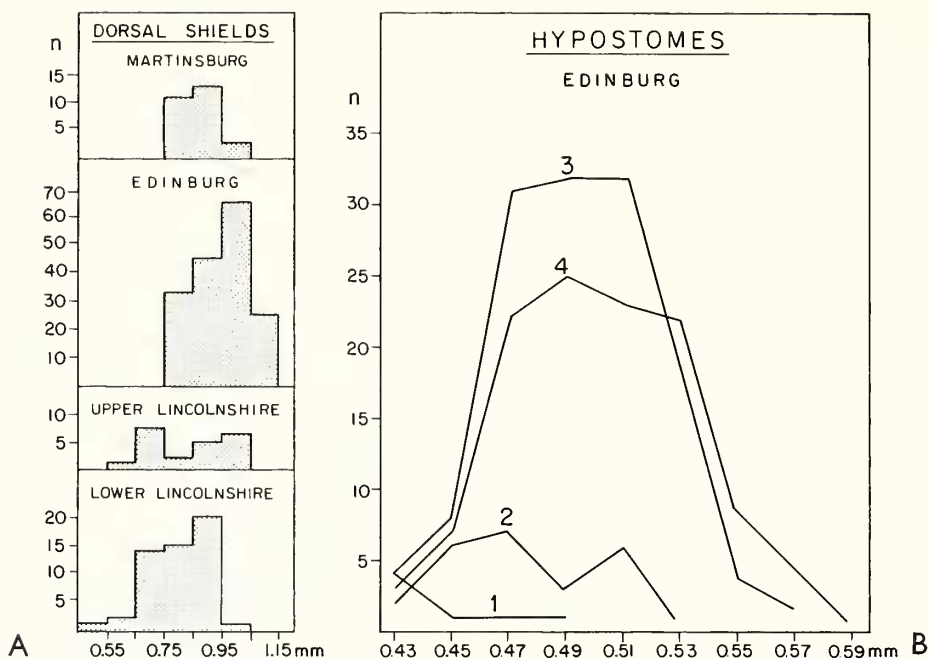
## THE DEVELOPMENT OF *ISOTELUS*

### *Protaspides*

Evitt (1961, pp. 988-990) described the earliest and latest stages of the protaspis period, and illustrated intermediate stages; his text-figs. 1-3 are partly based on more than one species. Four moults in the protaspis period are defined by coordinated and progressive changes affecting the

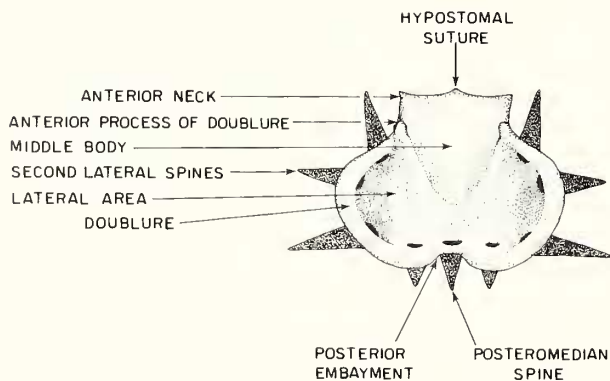
TABLE 1. Comparative frequency of occurrence of species described: vc, very common (more than 100 specimens); c, common (10-100 specimens); r, rare (1-9 specimens).

Formation	Lincolnshire		Edinburg	Oranda	Martinsburg	
	lower	upper				
<i>Isotelus</i>	sp. A	sp. B	<i>giselae</i>	sp. C	sp. D	sp. E
protaspides	c	c	vc	r	r	c
meraspides	c	c	vc	r	c	r
holaspides	r	r	c	r	c	r
<i>Nahannia</i>	sp.	sp.				
meraspides	r	r				
holaspides	—	r				



TEXT-FIG. 1. A, *Isotelus* spp., length (mm)/frequency histograms of protaspis dorsal shields from the lower and upper Lincolnshire, Edinburg, and Martinsburg formations. B, *I. giselae* sp. nov., width (tr.)/frequency distribution of protaspis hypostomes, Stages 1-4, from the Edinburg Formation, locs. 3 and 4 (Evitt Collection).

ten hypostomal characters listed on Table 2. In summary, Stage 1 is distinguished by the fused hypostomal suture, stumpy lateral and posteromedian spines, and rounded outline; Stage 2 by the abaxially open hypostomal suture and longer spines; Stage 3 by the tripartite open hypostomal suture, longer and more divergent lateral spines, and more oval outline; and Stage 4 by the bipartite open hypostomal suture, the posteromedian notch, and elongated posterior (fourth) lateral spines parallel to and matching the posteromedian spine. The hypostome became relatively smaller compared with the size of the dorsal shield in successive stages, with the result that the smallest hypostomes of each stage are the same size, but there is an increase in size range and average size (text-fig. 1B). Changes in the librigenae are described in the systematic descriptions below.



TEXT-FIG. 2. Terminology applied to parts of the *Isotelus* protaspis hypostome (dorsal view of Stage 4).

Dorsal shields can only be distinguished as early or late, based on size, development of the glabella, and the course of the facial suture; the only present/absent feature is the bifid posteromedian cusp in the late stage (coaptative with the studs at the tips of the librigenae), but this is seen only in well-preserved specimens. There is no discontinuity in the size/frequency charts (text-fig. 1A), and the stages evidently overlapped in size.

Early and late protaspis dorsal shields from the lower and upper Lincolnshire and Martinsburg Formations are compared with those from the Edinburg Formation on Table 3. All are strongly convex, and possess pairs of anterior and posterior spines. The differences between protaspides of the different species are considerable, affecting size, outline, convexity, strength of axial furrows, and length and position of the anterior and posterior spines, and are greater than at any subsequent stage.

A few protaspis hypostomes are known from the lower Lincolnshire and Martinsburg Formations; these conform to the four stages of the Edinburg material in the features summarized above, but with differences in other characters, such as the claw-like lateral spines of the Stage 1 hypostome from the Lincolnshire Formation (Pl. 54, fig. 1) and the deep doublure of the Stage 4 hypostome from the Martinsburg Formation (Pl. 54, fig. 20).

Early and late stages of protaspis dorsal shields and ventral plates were recognized in *I. parvirugosus* Chatterton and Ludvigsen, 1976, by Chatterton (1980, pl. 2, figs. 1–11, 16, 30; pl. 3, figs. 5–14; text-fig. 3D, E). The general development of the ventral plate is comparable to that of the Edinburg Formation material, albeit with strong specific characters. The protaspis dorsal shield differs markedly from all the species described herein in lacking marginal spines, and librigenae differ in outline. We have examined the protaspides from the Eden Formation, western Covington, Kentucky, illustrated by Hu (1971, pl. 26, figs. 17–21; text-fig. 57A–D); these differ markedly from known *Isotelus* protaspides in their weak convexity and in other features.

#### *Gap in the ontogenetic series*

Evitt (1961, p. 991) described in detail the striking difference in gross morphology between protaspides and meraspides of *Isotelus*; his observations have been confirmed in *I. parvirugosus* by Chatterton (1980). The largest protaspis from the Edinburg Formation is 1.13 mm long; the degree zero meraspis must have been about 2.0 mm long (Pl. 56, fig. 17; text-fig. 4). This gap between protaspis and meraspis is exceptionally great amongst trilobites. Evitt suggested two possible explanations; Chatterton (1980, p. 17) supported the first, that the young asaphid passed through a metamorphosis during which greatly accelerated development was incompletely recorded in moulted exoskeletons, commenting: 'The gap could be either caused by a period of rapid growth during this metamorphosis, or a longer period without forming a new exoskeleton during ecdysis.' Evitt drew attention to the resemblance between asaphid and remopleuridid protaspides, but demonstrated that the discontinuity was much greater in the asaphid (*Isotelus*) ontogeny.

#### *Meraspides*

Differences between meraspides described herein are summarized on Table 3. The following changes occur in all known ontogenies of *Isotelus*. 1, cranium: in the smallest cranidia the glabella is narrow; preglabellar, axial, and occipital furrows are strongly defined; with growth the glabella widens, the occipital furrow is effaced, and the preglabellar furrow becomes shallower; in the smallest cranidia L1 is well defined, more strongly adaxially than abaxially; in successive moults the axial furrow deepens and S1 dies out, L1 being almost completely fused in the effaced glabella; the palpebral lobe becomes shorter, the anterior extremity shifting further back; both anterior and posterior branches of the facial suture become more divergent. 2, librigena: in the smallest specimens the vincular socket and panderian opening are absent; the socket starts to develop at an estimated cephalic length of 4.5 mm; the inclination becomes steeper, the eye becomes shorter, and the doublure becomes more narrow. 3, hypostome: becomes wider in proportions, and the posteromedian notch becomes longer; the shoulder spine becomes less prominent and is finally lost. 4, transitory pygidium: becomes more elongate in proportions; the posteromedian notch, 10% the length of the transitory pygidium in the smallest specimens, is steadily reduced until lost at a pygidial length of about 2.3 mm.

Superimposed on this shared pattern of development, the following are the main characters which differ between species. 1, cranium: proportions; width of prelabellar field; presence of an anteromedian ridge; size, position, and slope of the palpebral lobe. 2, librigena: width of border; degree to which the border furrow is retained; length of genal spines at comparable sizes. 3, hypostome: length and outline of the posteromedian notch; development of the posterior wing; sculpture and extent of the finely striate, bevelled inner slope of the doublure of the posterior fork. 4, transitory pygidium: proportions; convexity; strength of furrows. In addition, the size at which changes in morphology take place varies between species (Table 3).

The morphological developments outlined above were completed at an estimated skeletal length of 9.0 mm in *I. giselae*; this compares with a skeletal length of 9.43 mm for the smallest recorded holaspis of *I. gigas* Dekay (Whittington 1957, p. 445). The sagittal length of the dorsal shield of *I. giselae* as represented by the largest known part (Pl. 57, fig. 16) is estimated at 100 mm., an increase in size of 130-fold throughout life.

#### SYSTEMATIC PALAEOLOGY

*Repositories of specimens.* BMNH, British Museum (Natural History), London; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; Geological Museum, University of Cincinnati, Ohio; Hunterian Museum, Glasgow University.

*Locality data.* Locality numbers are those of localities described by Whittington (1959) and Evitt (1953, 1961).

Family ASAPHIDAE Burmeister, 1843  
Subfamily ISOTELINAE Angelin, 1854  
Genus ISOTELUS Dekay, 1824

*Type species.* *I. gigas* Dekay, 1824, Sherman Fall Formation, Trenton Falls, New York, U.S.A.

*Discussion.* Formerly all the species described below would have been referred to *Homotelus*. Raymond (1920, p. 285) founded the genus *Homotelus* to include species which differed from typical *Isotelus* in lacking the concave lateral depression; he selected *H. ulrichi* Raymond, 1920, as type, a species in which the cephalic marginal depression is effaced mesially but is present laterally (Whittington 1950, p. 552, pl. 73, fig. 5). Whittington, De Mott (1963, p. 80), and Shaw (1968, p. 62) agreed on the unreliability of the partial absence of the lateral depression as a generic

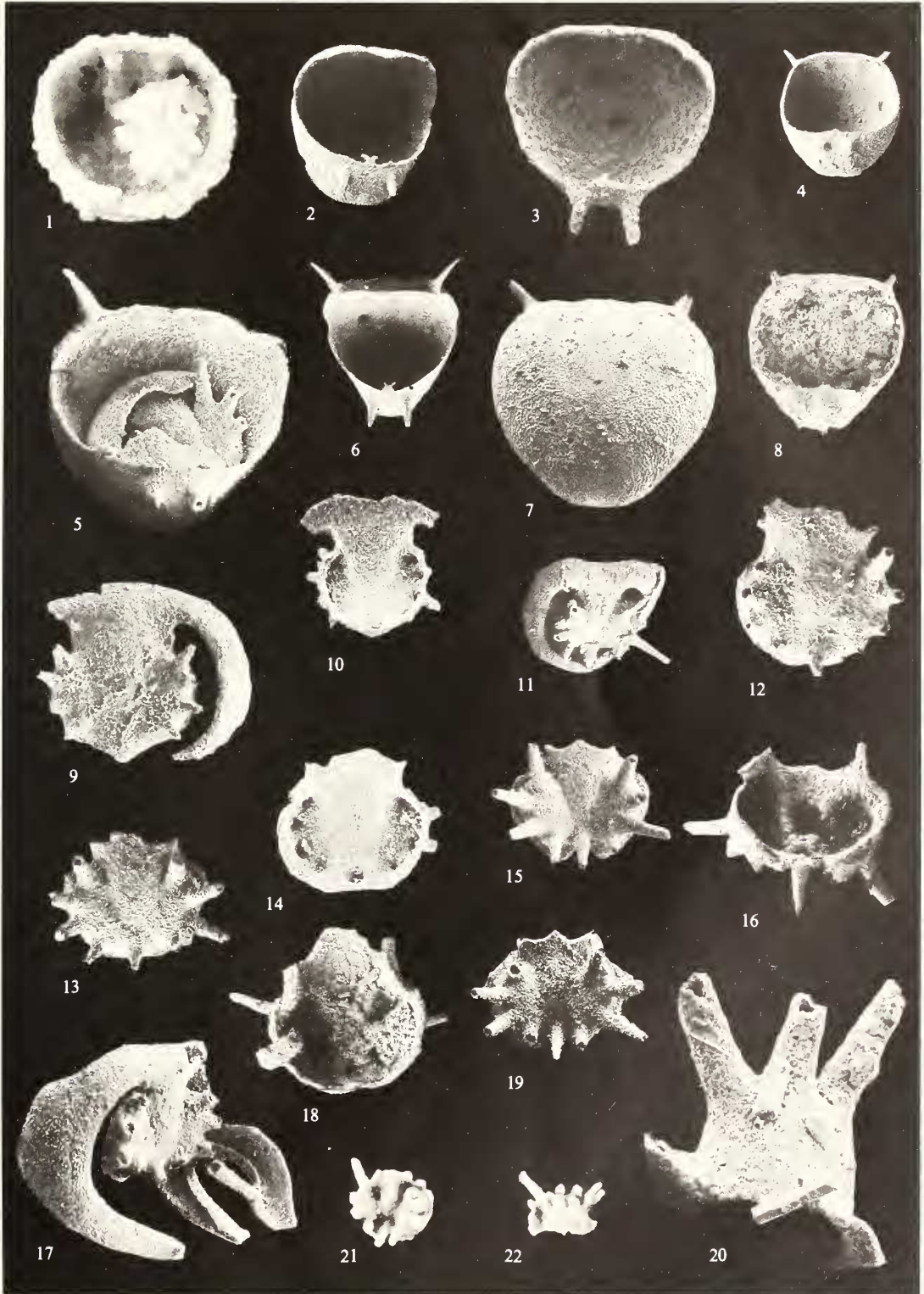
#### EXPLANATION OF PLATE 54

Figs. 1-8. *Isotelus* protaspis dorsal shields. 1 and 2, *I. sp. A*, lower Lincolnshire Formation, loc. 1; 1, It 20000, Stage 1, with incomplete ventral plate adhering to inner surface, ventral view,  $\times 55$ ; 2, It 17276, late stage, ventral view,  $\times 25$ . 3 and 4, *I. sp. B*, upper Lincolnshire Formation, loc. 1a: 3, It 17286, early stage, ventral view,  $\times 50$ ; 4, It 17284, late stage, ventral view,  $\times 25$ . 5 and 6, *I. giselae* sp. nov., Edinburg Formation: 5, It 17319, loc. 2, Stage 2, with incomplete ventral plate adhering to inner surface, ventral view,  $\times 50$ ; 6, It 17308, loc. 2, late stage, ventral view,  $\times 25$ . 7 and 8, *I. sp. E*, Martinsburg Formation, loc. 9: 7, It 17350, early stage, dorsal view,  $\times 50$ ; 8, It 17351, late stage, ventral view,  $\times 25$ .

Figs. 9-22. *Isotelus* protaspis ventral plates. 9-17, *I. giselae* sp. nov., Edinburg Formation, loc. 3 except fig. 17 (loc. 4): 9, It 17328, Stage 1, ventral view,  $\times 50$ ; 10, It 17325, Stage 1, dorsal view,  $\times 25$ ; 11, It 17337, Stage 2, ventral view,  $\times 25$ ; 12, It 17326, Stage 2, ventral view,  $\times 50$ ; 13, It 17324, Stage 3, ventral view,  $\times 50$ ; 14, It 17315, Stage 3, dorsal view,  $\times 50$ ; 15, It 17322, Stage 4, ventral view,  $\times 50$ ; 16, It 17336, Stage 4, dorsal view,  $\times 50$ ; 17, It 17331, Stage 4, oblique ventral view (note ventral stud at tip of librigena),  $\times 50$ . 18-20, *I. sp. E*, Martinsburg Formation, loc. 10 except fig. 20 (loc. 12): 18, It 17354, Stage 3, dorsal view,  $\times 50$ ; 19, It 17355, Stage 4, oblique ventral view,  $\times 50$ ; 20, It 17361, Stage 4, oblique ventral view showing deep doublure, resembling a lateral border,  $\times 135$ . 21 and 22, *I. sp. A*, lower Lincolnshire Formation, loc. 1, specimen lost, ventral and left lateral views,  $\times 36$ .

Figs. 1, 21, 22, light micrographs by W. R. E. of whitened specimens; all others SEM micrographs. All BMNH specimens except figs. 21, 22.





criterion, and suggest the abandonment of *Homotelus*; the evidence of the species described herein supports this view.

*Isotelus giselae* sp. nov.

Plate 54, figs. 5, 6, 9-17; Plate 56, figs. 9-17; Plate 57, figs. 10-13, 15-18; text-figs. 3, 4, 5A-C, 6A

1942 *Homotelus simplex* (Raymond and Narraway); Butts, pl. 101, figs. 27, 28.

1961 asaphid indet., Evitt, p. 988, pl. 117, figs. 5-16, 19-21; pl. 118, figs. 1-34, 37-39.

1975 *Remopleurides caelatus* Whittington; Hu, pl. 2, figs. 3, 4, 6, 7, 20; pl. 3, figs. 21, 22, text-fig. 1C-E, G.

1975 *Isotelus* sp., Hu, p. 41, pl. 4, figs. 12-15, 20-23, 25, 26, 28-33; text-fig. 3H, M, N, P-S.

*Derivation of name.* After Mrs. W. R. Evitt who, in sorting fine residues, was the first to suspect the true association of parts of the asaphid protaspis.

*Diagnosis.* Lateral depression of exoskeleton indistinct, absent mesially. Minimum width of cranidium (at anterior extremities of palpebral lobes) 65-70 % sagittal length, and situated opposite midlength of cranidium. Palpebral lobe strongly elevated. Librigenal spine absent in full-grown cephalo. Hypostome strongly sculptured.

*Holotype.* USNM 398481 (inner layer of silicified cranidium, text-fig. 5A-C), locality 2 (Crabill Farm), Strasburg, Virginia, USA; Lantz Mill facies, Edinburg Formation, Middle Ordovician. Collected by Mr Y. Kirkpatrick-Howat. The dimensions of the holotype cranidium are: length, 20.8 mm; minimum width (at anterior extremity of palpebral lobe), 14.6 mm; maximum preocular width, 16.1 mm; estimated width across palpebral lobes, 21.0 mm; estimated width at posterior margin, 30.0 mm.

*Other material.* See Plate explanations for specimen details. Locs. 2-7, 14, and 0.6 km SE of Willow Grove Station, 4.8 km SW of Woodstock; Edinburg Formation, Middle Ordovician.

*Description.* Cranidium gently convex, minimum width (at anterior extremity of palpebral lobe) 65-70 % sagittal length and 80-90 % maximum preocular width, situated opposite midlength of cranidium. Glabella fused with occipital ring, narrowing forwards to 65 % of its posterior width opposite anterior extremity of palpebral lobe, widening and becoming undefined anteriorly. Lateral glabellar lobes and furrows faintly impressed on holotype cranidium (in which only the inner layer of quartz is preserved): S1 short and strongly oblique, S2 and S3 short transverse. Shallow abaxial preglabellar and occipital furrows distinguishable on holotype, plus a small posteromedian tubercle. Axial furrow broad and shallow posteriorly, dying out anterior to palpebral lobe. Basal apodemes small, rounded, 50 % maximum width of cranidium apart. Fixigena broad (tr.) posteriorly, exceptionally so on holotype, in which width between sutures at posterior margin estimated at 140 % length (sag.) of cranidium. Palpebral lobe 10 % cranial length, posterior extremities slightly further apart than anterior; lobe strongly elevated, as tall as long (exsag.), sloping inwards with increasing steepness. Posterior border furrow effaced. Anterior branches of facial sutures diverge strongly outwards and forwards from eyes to 90 % width across palpebral lobes, opposite 30-35 % sagittal length of cranidium from front, thence curving inwards to midpoint intramarginally. Posterior branch curves gently outwards and backwards, at 50° to sagittal axis. External surface smooth or faintly pitted. Doublure of glabella comparatively short, narrowing out abaxially. Doublure of posterior border absent except for triangular area laterally.

Largest librigena BMNH It 18810 (Pl. 57, fig. 15), appropriate to a cephalon 26 mm in estimated length, slopes steeply outwards with even convexity; lateral border not demarcated. Eye not preserved. Subocular furrow broad and shallow. Lateral border absent. Genal angle narrowly rounded. Median connective suture open. External surface smooth or faintly pitted. Doublure 35 % cephalic length, horizontal, flattened; inner margin broadly embayed mesially to accommodate hypostome, forming cusp opposite anterior extremity of eye, thence curving inwards and backwards and bending inwards posteriorly to meet lateral doublure of posterior border of cranidium. Lateral depression narrows and deepens backwards, terminating abruptly in a vincular socket at 20 % estimated cephalic length anterior to genal angle. Panderian process represented by a thinning in test, often incompletely silicified, a short distance posterior and adaxial to vincular socket. Terrace lines strong, closely spaced, running parallel to adjacent margin, absent in vincular socket. Adult librigenae (Pl. 57, fig. 11) up to 22 mm in estimated cephalic length, retain slender genal spine estimated at about 35 % length (sag.) of cephalon.

Largest hypostome BMNH It 18814 (Pl. 57, figs. 12, 13) 9.7 mm long (exsag.), as long as wide, weakly

convex. Anterior margin transverse mesially, curving downwards and backwards at subtrapezoidal anterior wing. Lateral margin strongly rounded. Middle body undefined, without independent convexity. Macula smooth, depressed, gently swollen, transversely oval, at 30 % length from front, 50 % maximum width of hypostome apart, rarely preserved. Median notch 45 % length (exsag.) of hypostome. Posterior fork narrows steadily backwards, tips 50 % maximum width of hypostome apart. Posteriorly, inner margin of fork diverges backwards at 20° to midline, slightly less divergent at front. Ventral surface with terrace lines as follows: wavy, transverse lines on middle body; fourteen or fifteen longitudinal lines abaxially; lateral seven or eight extend successively further beyond macula, running parallel to lateral margin; nine or ten lines parallel to apex of median notch; posteriorly and adaxially widely spaced faint lines branch to form faint network. Anterior margin of doublure transverse for 45 % width of hypostome just anterior to median notch, bending forwards sharply and extending forward to anterior wing abaxially. Posterior wing process just anterior to bend projects laterally and dorsally as a tongue-shaped projection. Doublure beneath fork swollen to form keel curving forwards from tip and slightly outwards, dying out anteriorly; inner slope flat, with about fifty faint, closely spaced, straight, parallel striae running aslant bevelled face, curving forwards near crest of keel; outer slope convex, with a few widely spaced raised lines.

Number of thoracic segments unknown. Axis 40–45 % width of thorax, convex transversely. Axial furrow shallow. Pleural lobe downturned at fulcrum; articulating facet strong, marked off by faint, oblique furrow. Pleural furrow shallow, running obliquely from inner anterior corner, dying out at fulcrum. Articulating half ring short, ring furrow shallow; apodeme at abaxial extremity. Axial doublure about half length of ring. Pleural doublure about 50 % width to fulcrum for most of length, inner margin sinuously longitudinal. Terrace lines parallel to margin and closely spaced adaxially, oblique and widely spaced for most of width. Panderian

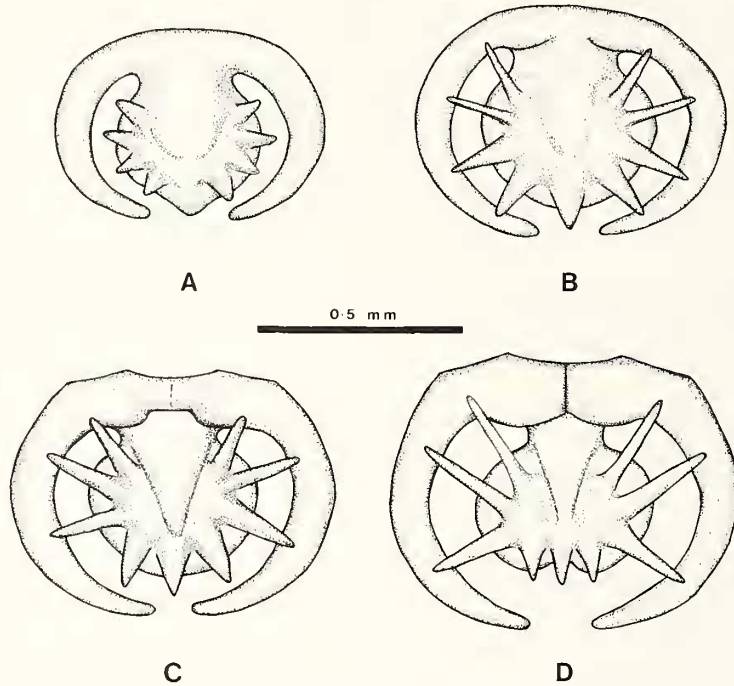
TABLE 2. *Isotelus giselae* sp. nov. Edinburg Formation. Stages in the development of the protaspis librigena and hypostome.

	Stage 1	Stage 2	Stage 3	Stage 4
<b>LIBRIGENA</b>				
connective suture	fused	fused	partly fused	open
ventral stud at tip	absent	absent	present	present
(width between extremities)	40	20	5	5
% (maximum width across plate)				
<b>HYPOSTOME</b>				
width (mm)	0.43–0.49	0.43–0.53	0.43–0.57	0.43–0.59
mean width (mm)	0.45	0.48	0.49	0.50
number of specimens	7	23	131	94
(width) % (maximum width across ventral plate)	55	55	50	50
hypostomal suture	fused	partly fused	tripartite	bipartite
(width of neck) % (width of hypostome)	70	60	55	50
middle body	large	narrower	smaller	small, convex
hindmost lateral spine	very short	short, divergent	long, divergent	long, longitudinal
posteromedian projection	blunt	stumpy spine	short spine	long, steep spine
posteromedian outline	bowed backwards	convex backwards	rounded	notched
height	shallow	shallow	deep	deep
anterior process on doublure	absent	absent	small	long
thickness of test	thin	thin	thick	thick
<b>ILLUSTRATIONS</b>				
Evitt 1961, pl. 117, fig.				19
Evitt 1961, pl. 118, figs.	18, 22–24	25, 26	27–29	21, 30–34, 37–39
Hu 1975, pl. 2, fig.	20			
this paper, text-fig. 3	A	B	C	D
this paper, Pl. 54, figs.	9, 10	11, 12	13, 14	15–17



opening adaxial to midwidth and anterior to midlength, covered by backwardly facing cowl. Doublure widens abruptly at back, extending to 75 % width to fulcrum, narrowing out adaxially.

Largest pygidium BMNH It 18813 (Pl. 57, fig. 16) 68 mm wide, incomplete posteriorly, but approximately 60 % as long as wide, gently convex. Axis extremely ill defined, 30 % maximum width of pygidium anteriorly. Axial furrow faint and broad, running inwards and backwards at 20° to midline. Articulating half ring and furrow short. Pleural lobe evenly and gently convex, with no change of convexity at border. Anterolateral facet strongly developed and extending for half width of pleural lobe. First pleural furrow deep and broad,



TEXT-FIG. 3. *Isotelus giselae* sp. nov., Edinburg Formation, locs. 3 and 4, protaspis ventral plates. A, Stage 1, hypostomal suture entirely fused. B, Stage 2, hypostomal suture fused mesially, functional laterally. C, Stage 3, hypostomal suture tripartite and functional. D, Stage 4, hypostomal suture bipartite.

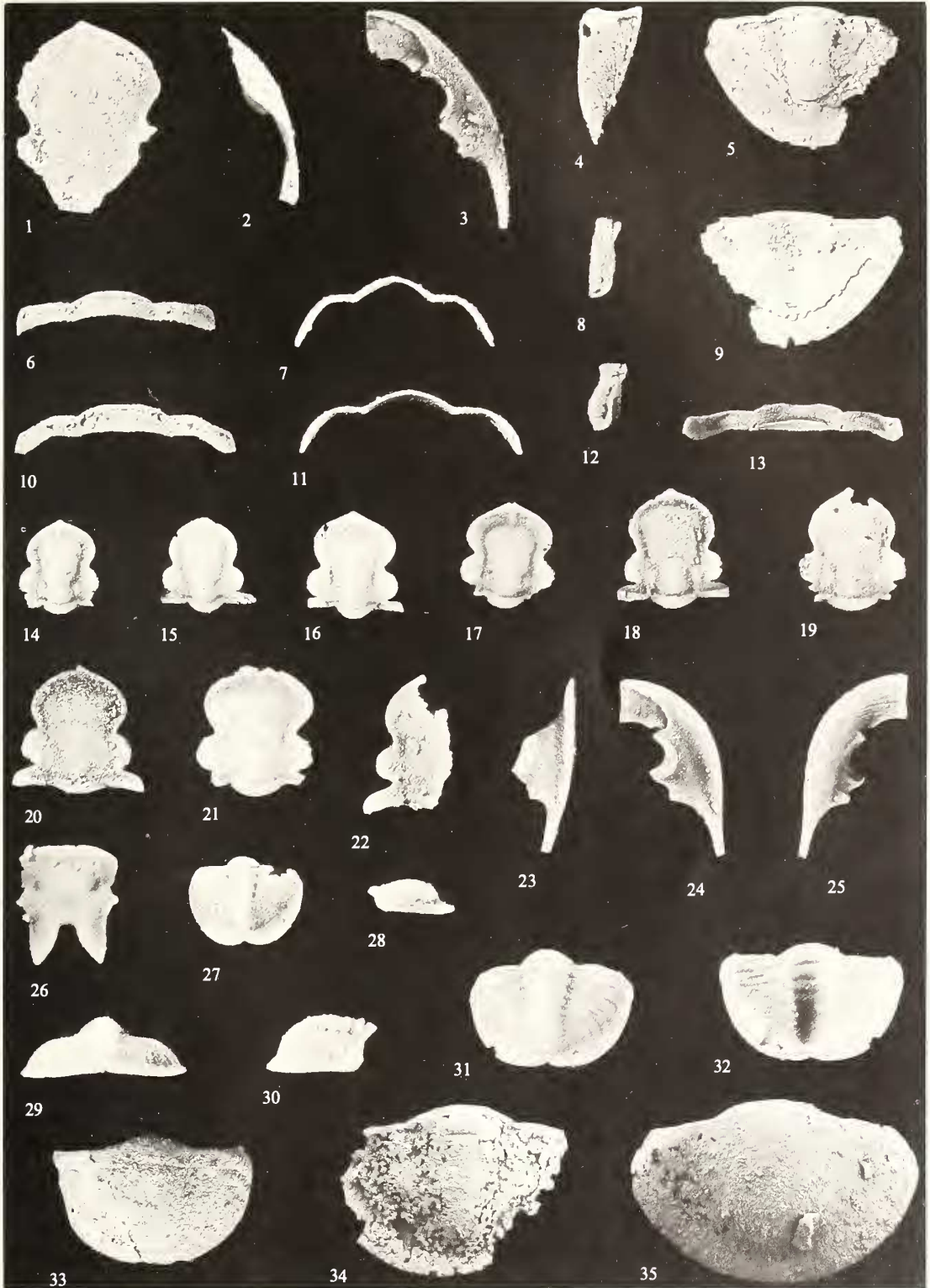
#### EXPLANATION OF PLATE 55

Figs. 1–32. *Isotelus* sp. A, lower Lincolnshire Formation, loc. 1. 1–13, holaspides: 1 and 2, USNM 258078, cranium, dorsal and left lateral views,  $\times 8$ ; 3, USNM 258079, right librigena,  $\times 8$ ; 4, 5, 9, USNM 258080, pygidium, left lateral, dorsal, and ventral views,  $\times 8$ ; 6–8, USNM 258081, thoracic segment, dorsal, posterior, and right lateral views,  $\times 6$ –6; 10–13, USNM 258082, thoracic segment, dorsal, posterior, right lateral, and ventral views,  $\times 6$ –4. 14–32, meraspides: 14–22, USNM 258083–258090, crania showing progressive effacement of anteromedian ridge and the preglabellar, occipital, and S1 furrows, all  $\times 10$ ; 23–25, USNM 258091, right librigena, right lateral, dorsal, and ventral views,  $\times 10$ ; 26, USNM 258092, hypostome,  $\times 24$ ; 27 and 28, USNM 258093, transitory pygidium,  $\times 14$ ; 29–32, USNM 258094, transitory pygidium, posterior, right lateral, and dorsal views,  $\times 12$ , ventral view,  $\times 13$ .

Figs. 33–35. *Nahannia* sp. 33, BMNH It 17277, lower Lincolnshire Formation, loc. 1, transitory pygidium,  $\times 10$ . 34 and 35, upper Lincolnshire Formation, loc. 1a, small pygidia: 34, BMNH It 17304,  $\times 10$ ; 35, BMNH It 17305,  $\times 10$ .

Figs. 1–32, light micrographs by W. R. E.; figs. 33–35, SEM micrographs.





marking off a swollen first half-pleura. Six short, unfurrowed pleural ribs, dying out before midwidth of pleural lobe; rib furrows successively shorter and fainter towards back. External surface smooth. Doublure of uniform width, 25 % length of pygidium at sagittal axis; anterior margin simply rounded, not embayed mesially. Elongate process at anterolateral corner (fitting with vincular notch of librigena). Terrace lines faint, running subparallel to margin. Smaller pygidia relatively narrower, 65 % as long as wide, axis 80 % length (Hu 1975, pl. 4, figs. 30, 32, 33).

*Description of protaspis ventral plates.* Stage 1 (Pl. 54, figs. 9, 10). Librigenae and hypostome fused; median connective and hypostomal sutures absent. Width of librigena at midlength 10 % width of ventral plate. Librigena narrows steadily backwards, distance between tips 40 % width across ventral plate. Hypostome 0.43–0.49 mm wide (all hypostomal width measurements exclude lateral spines), 55 % maximum width of ventral plate. Neck continuous with librigena, 70 % width of hypostome. Middle body large with slight independent convexity. Lateral area crescentic in outline, sloping slightly inwards. Four outwardly directed lateral spines, length one to three times basal width, subequal in size. Posteromedian margin projects backwards in blunt, broad-based marginal projection. Doublure shallow, almost vertical, continuous with narrow doublure of librigena; anterior dorsal process absent. Test thin. Surface smooth.

Stage 2 (Pl. 54, figs. 11 and 12). Differs from Stage 1 as follows. Librigenae and hypostome fused mesially; median connective suture absent; hypostomal suture open laterally, curving outwards and backwards. Distance between tips of librigenae 20 % maximum width of ventral plate. Hypostome 0.43–0.53 mm wide, neck 60 % width of hypostome. Middle body smaller and more strongly defined. Lateral spines more erect and more splayed, length four to five times basal width. Posteromedian outline rounded; posteromedian spine as wide as long, projecting outwards and upwards at base of neck.

Stage 3 (Pl. 54, figs. 13 and 14). Median connective suture partially fused. Distance between tips of librigenae 5 % maximum width of ventral plate. Small rounded stud at tip of librigena projects ventrally (fitting with bifid process on posteromedian margin of dorsal shield). Hypostomal suture open (occasionally secondarily fused), tripartite, transverse mesially, concave forwards laterally. Hypostome 0.43–0.57 mm wide, 50 % maximum width of ventral plate. Neck 55 % width of hypostome. Middle body narrower. Lateral area slopes more strongly inwards. Lateral spines more erect, more splayed, hindmost (fourth from front) divergent. Posteromedian spine longer. Doublure deeper, narrowing out at base of neck where dorsal projection larger. Test thicker.

Stage 4 (Pl. 54, figs. 15–17). Median connective suture open. Hypostomal suture bipartite and monocuspid. Ventral stud at tip of librigena larger (Pl. 54, fig. 17). Hypostome 0.43–0.59 mm wide, 50 % maximum width of ventral plate. Neck 50 % width of hypostome. Middle body smaller and more convex. Posteromedian spine longer, more slender, and sloping forwards more steeply. Fourth lateral spine parallel and equal to posteromedian spine in slope and length. Posterior outline of doublure notched for 25 % maximum width of hypostome; anterolateral projection longer and stouter.

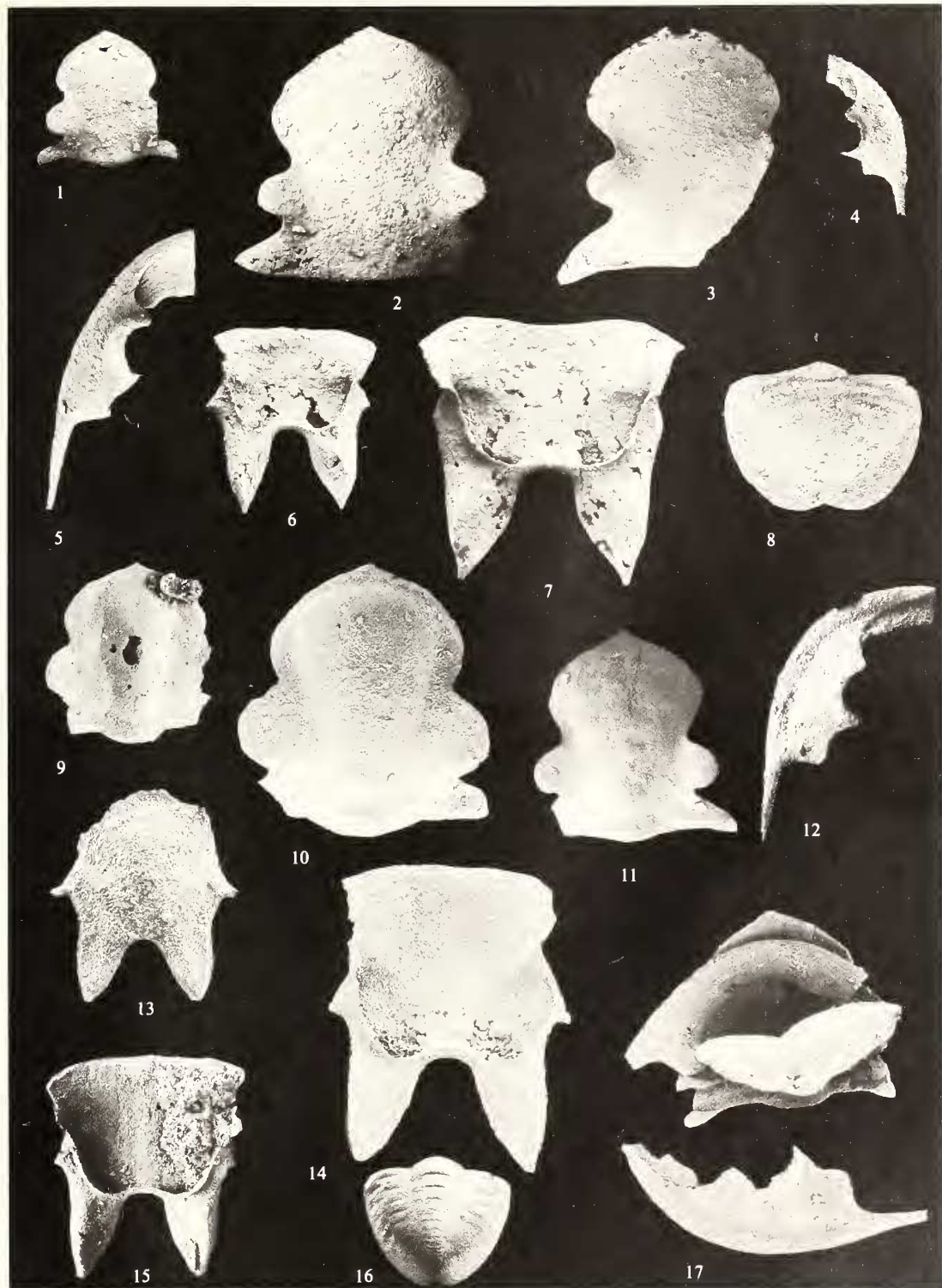
*Description of protaspis dorsal shields.* Early stages (1 and 2). Dorsal shield BMNH It 17319 (Pl. 54, fig. 5) length 0.75–c.0.85 mm, almost as long as wide, strongly convex, recurved for about 40 % length (sag.); anterior margin simple, convex forwards; posterior margin monocuspid forwards. Glabella short, with slight independent convexity. Axial furrow indistinct, but represented by pit at 10 % length of protaspis from front. Anterior spine horizontal, 25 % length of protaspis, tips at 95 % width of protaspis apart, slender, diverging forwards at 35° to midline. Posterior spine directed longitudinally, 25 % length of protaspis, sloping ventrally at 40° to plane of anterior spine, tips at 30 % width of protaspis from midline. Librigena ventral except for small anterolateral surface, without eye.

#### EXPLANATION OF PLATE 56

Figs. 1–8. *Isotelus* sp. B, upper Lincolnshire Formation, loc. 1a; meraspides except fig. 3. 1–3, cranidia: 1, It 17219,  $\times 10$ ; 2, It 17291,  $\times 10$ ; 3, It 17292, small holaspis,  $\times 10$ . 4 and 5, right and left librigenae; 4, It 17306,  $\times 10$ ; 5, It 17293,  $\times 10$ . 6 and 7, hypostomes, dorsal views: 6, It 17297,  $\times 25$ ; 7, It 17298,  $\times 25$ . 8, It 17300, transitory pygidium,  $\times 25$ .

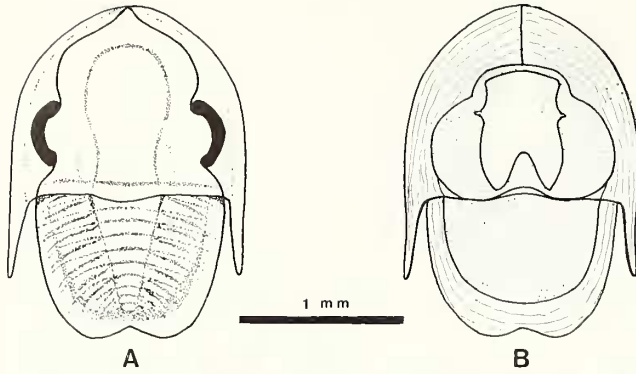
Figs. 9–17. *I. gisetae* sp. nov., Edinburg Formation, loc. 3, except fig. 14 (loc. 4), meraspides. 9–11, cranidia: 9, It 17339,  $\times 25$ ; 10, It 17344,  $\times 25$ ; 11, It 17343,  $\times 10$ . 12, It 17349, left librigena,  $\times 25$ . 13–15, hypostomes: 13, It 17340, dorsal view,  $\times 50$ ; 14, It 17341,  $\times 50$ ; 15, It 17338, ventral view,  $\times 25$ . 16, It 17347, transitory pygidium,  $\times 10$ . 17, It 17346, disassociated exoskeleton, probably degree zero,  $\times 25$ .

All SEM micrographs of BMNH specimens.

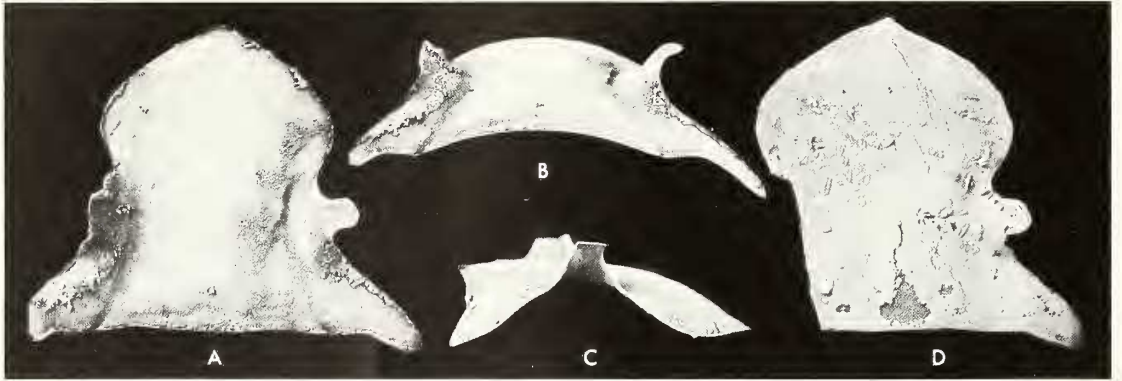


TRIPP and EVITT, *Isotelus*





TEXT-FIG. 4. Reconstruction of degree zero meraspis of *Isotelus giselae* sp. nov., Edinburg Formation, loc. 3. A, dorsal view. B, ventral view.



TEXT-FIG. 5. A - C, *Isotelus giselae* sp. nov., Edinburg Formation, loc. 2; USNM 398481 holotype cranidium, dorsal, posterior, and right lateral views,  $\times 2$ . D, *I.* sp. B, upper Lincolnshire Formation, loc. 1a; USNM 398482, cranidium,  $\times 1.5$ . Photographs prepared by the National Museum of Natural History, Washington.

Late stages (3 and 4). Dorsal shield (Pl. 54, fig. 6; Pl. 57, fig. 18) length c.0.80–1.13 mm, wider than early stage anteriorly, deeper posteriorly, anterior margin and outline more sinuous due to stronger development of glabella and facial suture; posterior margin with bifid median cusp (fitting with stud at tip of librigena). Glabella 20 % length of protaspis, with moderate independent convexity. Axial furrow shallow, deepening towards front, but shallowing near anterior margin. Anterior spine 30 % length of protaspis, slender, tips 110 % width of protaspis apart, diverging at  $45^\circ$  to midline. Posterior spine 30 % length of protaspis, directed downwards and slightly outwards at  $70^\circ$  to plane of anterior spine. Dorsal area of librigena larger, indenting anterolateral margin of dorsal shield.

*Description of meraspis.* Smallest cranidium BMNH It 17339 (Pl. 56, fig. 9) 1.1 mm long, minimum width 70 % sagittal length and 95 % maximum preocular width. Glabella circumscribed, gently convex, waisted near midlength, widening posteriorly, maximum preocular width 55 % length. Occipital ring more than 10 % length and 45 % preocular width of cranidium, bowed backwards. Occipital furrow broad and shallow. Axial furrow shallow anteriorly, deepening backwards. Preglabellar field 10 % length of cranidium. Fixigena weakly convex; L1 with slight independent convexity, 20 % length of cranidium. S1 much deeper than axial furrow alongside L1. Palpebral lobe 35 % cranial length, strongly rounded in outline, anterior extremity at 40 % length from front. Posterior border furrow shallow, continuous with lateral border furrow. Anterior branch of facial suture diverges forwards before curving inwards to midline. Posterior branch curves outwards and backwards. Doublure of occipital ring extends half way to occipital furrow; doublure of posterior border absent adaxially, developing abaxially. Cranidium BMNH It 17344 (Pl. 56, fig. 10) 1.7 mm long, minimum width 60 % sagittal length and 80 % maximum preocular width. Glabella convex, clearly defined, narrowing backwards. Occipital



ring 60 % preocular width of cranidium. L1 and S1 distinct, but less well defined. Palpebral lobe 35 % cranial length, anterior extremity opposite midlength of cranidium. Indistinct preoccipital tubercle slightly off-centre, present only on this specimen. Cranidium BMNH It 17343 (Pl. 56, fig. 11) 3.1 mm long, preocular width 85 % palpebral width. Glabella defined anteriorly only by change in convexity. Axial furrow deepens backwards. Occipital ring 65 % preocular width of cranidium. Occipital furrow faint. S1 effaced. Palpebral lobe 25 % length (sag.) of cranidium.

Smallest librigena BMNH It 17349 (Pl. 56, fig. 12) 1.1 mm estimated cephalic length, wide, sloping gently outwards. Eye rounded in outline, not marked off from cheek, convex. Lateral border uniformly narrow, half width of field opposite eye, continuous with posterior border and genal spine. Genal spine slender, pointed, 45 % estimated length of cephalon. Doublure 20 % estimated length of cephalon mesially, wide, inner margin curving backwards and inwards, forming a cusp, thence curving outwards and backwards, bending strongly inwards posteriorly to abut against abaxial doublure of posterior border of cranidium; vincular socket and panderian opening absent. With increase in size librigena slopes more steeply outwards, narrower; lateral border furrow obsolete. Vincular socket develops slowly between lengths 4.5 mm and 6.0 mm.

Smallest hypostome BMNH It 17340 (Pl. 56, fig. 13) 0.65 mm long (exsag.), 85 % as wide as long. Anterior margin broadly rounded. Middle body weakly swollen; middle furrow at 35 % length from front, running for a short distance inwards and backwards, more distinct on internal than on external surface; posterior lobe triangular, with slight independent convexity, 30 % width of hypostome. Lateral border runs longitudinally; shoulder forms prominent outwardly directed spine opposite midlength of hypostome. Posterior forks narrow steadily to acute points, 60 % width of hypostome apart. Median notch 30 % length (exsag.) of hypostome. Anterior margin of doublure convex forwards anterior to median notch, convex backwards at base of fork, curving obliquely forwards to anterior wing; posterolateral process absent; bevelled inner slope of fork striate. Hypostome BMNH It 17338 (Pl. 56, fig. 15) 1.4 mm long (exsag.), middle body and posterior lobe undefined, greatest width at anterior wing; shoulder spine less protuberant, cuspid. Median notch 35 % length (exsag.) of hypostome.

Smallest transitory pygidium 0.9 mm long, length 65 % width, convex, posteromedian notch 10 % length of pygidium. Axis 30 % maximum width and 85 % length, narrowing slowly backwards. Pleural lobe convex adaxially, with a concave area widening towards back abaxially. Eight segments, increasingly ill-defined towards back. Rib furrows broader but shorter than inter-rib furrows. Doublure extends in an even curve to tip of axis, lying close beneath dorsal surface; terrace lines faint and widely spaced. Transitory pygidium BMNH It 17347 (Pl. 56, fig. 16) 1.9 mm long (sag.), length 80 % width, posteromedian notch small, adaxial area of pleural lobe more strongly convex, five segments clearly defined. With increase in size to 2.3 mm, posteromedian notch dies out, and segmentation is effaced.

*Discussion.* All silicified material from the Edinburg Formation appears to belong to a single new species of *Isotelus*. The numerous protaspides from various localities conform closely with the figured specimens. The variation in meraspis cranidia is limited, e.g. a posteromedian tubercle is present on one specimen (BMNH It 17344; Pl. 56, fig. 10). Larger cranidia are closely similar in linear measurements, except that the holotype is comparatively broad. Librigenae are consistent in character, subject to changes with growth. All hypostomes are identical, even as regards the fine detail of the sculpture, and we regard this as weighty evidence. The single large incomplete pygidium BMNH It 18813 (Pl. 57, fig. 16), 68 mm in width, appears to have been shorter in proportions than smaller specimens; this difference might be attributable to growth, although Whittington (1957, p. 445, figs. 25–27) found that the proportions of *I. gigas* altered little with development.

The crack-out cranidium and pygidium illustrated by Butts (1942, pl. 101, figs. 27 and 28), from the Edinburg Formation, near Strasburg, appear to be conspecific with the silicified material, the only difference being that the axis of the pygidium is more strongly outlined.

Raymond (1920, p. 288; 1925, p. 88, pl. 4, figs. 1–3) described *Homotelus elongatus* from the Echinosphaerites and Nidulites Beds of the Edinburg Formation. *I. giselae* differs in having the palpebral lobe shorter (exsag.) and more strongly elevated, and the pygidium smooth, not pitted. Wilson (1947, p. 22, pl. 1, fig. 5) figured an extended dorsal shield from the Hull Beds at Chaudière Falls, Hull, Quebec, as *H.? elongatus* Raymond. This specimen differs from both *I. elongatus* and *I. giselae* in the more elongate and more convex pygidium.

*I. giselae* bears a general resemblance to *I. simplex* (Raymond and Narraway 1910, p. 51, pl. 16, figs. 6–8; De Mott 1963, pl. 4, figs. 1–22) from the Platteville Group, but differs conspicuously in the elevated palpebral lobes.

*I. parvirugosus* Chatterton and Ludvigsen (1976, p. 21, pl. 2, figs. 1–42) from the Esbataottine Formation, has similarly elevated palpebral lobes, but the presence of lateral and posterior cranial borders precludes any possibility of a close relationship to *I. giselae*. An occipital and three pairs of lateral glabellar furrows, comparable to those in our holotype, are distinguishable in *I. parvirugosus*.

*I. giselae* is similar to the type species, *I. gigas* Dekay (1824, p. 176, pl. 12, fig. 1; pl. 13, fig. 1), in eye position, in the absence of genal spines in the adult, and in hypostomal construction (Ross 1967, pl. 1, figs. 2, 6–9). *I. giselae* differs markedly in that the lateral depression is effaced, the cranidium expands more strongly anteriorly, the fixigena are much wider posteriorly, the eyes are elevated, and the pygidium is much wider.

#### *Isotelus* sp. A

Plate 54, figs. 1, 2, 21, 22; Plate 55, figs. 1–32

1950 hypostome indet., Evitt, pl. 2, figs. 17a–d.

1961 asaphid indet., Evitt, pl. 117, figs. 1–4; pl. 118, figs. 35, 36.

*Material.* See plate explanations for specimen details. Loc. 1, lower Lincolnshire Formation, Middle Ordovician.

*Description.* Differs from *I. giselae* as follows: palpebral lobes not elevated; hypostome (Evitt 1961, pl. 118, fig. 36) with tips of forks 55% (cf. 50%) maximum width of hypostome apart and longitudinal (cf. transverse) raised lines on the middle body.

The smallest protaspis, BMNH It 20000, is a dorsal shield 0.5 mm in length, with the hypostome (fused to part of the librigena) adhering to the inner surface (Pl. 54, fig. 1). The hypostome shows the distinctive features of Stage 1 as described in the Edinburg Formation material, particularly the short lateral spines, stumpy posteromedian spine, and broad neck fused with the librigenae. Interestingly, it differs significantly and recognizably in the short, claw-like, first and second lateral spines. A single hypostome with the posteromedian notch of Stage 4 is illustrated (Pl. 54, figs. 21, 22). Dorsal shields of late protaspides differ from *I. giselae* in size range (Table 3), longer axial furrows, and shorter marginal spines, placed closer together.

A comparison of meraspides with other species described herein is summarized in Table 3. The series of meraspis cranidia illustrated (Pl. 55, figs. 14–22) clearly demonstrates the gradual effacement of the preglabellar, occipital, and S1 furrows, and fusion of L1 with the rest of the glabella. The most distinctive feature is the strong anteromedian ridge in small meraspis cranidia, which is gradually effaced with growth. This ridge is much longer in some specimens (Pl. 55, figs. 16 and 17) than in others, but we consider this to be only a variational distinction.

*Discussion.* The cranidium not quite 4.0 mm in sagittal length (Pl. 55, figs. 1 and 2) is by far the largest, though fragments indicate larger individuals. Breakage was due to mechanical stresses before preservation, and was not the result of the recovery process—all the lower Lincolnshire trilobites show similar signs of fragmentation, the cause of which is not known. Not so in the Edinburg material, in which extremely careful etching has led to the recovery of a few large and articulated specimens.

#### EXPLANATION OF PLATE 57

Figs. 1–8, 14. *Isotelus* sp. D, Martinsburg Formation, loc. 10a; meraspides except fig. 3. 1–3, cranidia: 1, It 17377,  $\times 25$ ; 2, It 17375,  $\times 10$ ; 3, It 17374, small holaspis,  $\times 5$ . 4, It 17382, right librigena, ventral view showing absence of vincular notch,  $\times 10$ . 5, It 17372, hypostome, ventral view,  $\times 10$ . 6 and 7, transitory pygidia: 6, It 17379,  $\times 25$ ; 7, It 17384,  $\times 10$ . 8, It 17385, right librigena, ventral view,  $\times 6$ . 14, It 17366, hypostome, ventral view,  $\times 5$ .

Fig. 9, *I.* sp. B, upper Lincolnshire Formation, loc. 1a; It 19068, cranidium, ventral view,  $\times 5$ .

Figs. 10–13, 15–18. *I. giselae* sp. nov., Edinburg Formation, loc. 3. 10, It 18811, cranidium,  $\times 2$ . 11, It 18812, largest librigena retaining genal spine, ventral view,  $\times 2$ . 12 and 13, It 18814, hypostome, ventral and dorsal views,  $\times 3$ . 15, It 18810, adult right librigena,  $\times 2$ . 16, It 18813, large pygidium,  $\times 1$ . 17, It 17345, small hypostome, dorsal view showing finely striated, bevelled inner slope of doublure of fork,  $\times 30$ . 18, It 17310, protaspis dorsal shield, ventral view, late stage,  $\times 30$ .

All SEM micrographs of BMNH specimens.





TABLE 3. *Isotelus* spp. from Virginia. Comparison of protaspides and meraspides. Averages of early and late stages are separated by a solidus.

Species	A	B	<i>giselae</i>	D
Formation	Lincolnshire		Edinburg	Martinsburg
	lower	upper		
<b>PROTASPIS</b>				
range in dorsal length (mm)	0.5/1.0	0.6/1.0	0.75/1.13	0.75/1.05
late protaspis: (length of axial furrow) % (length)	35	20	20	50
late protaspis: (length of spines) % (length)	10	20	25	20
(width between tips of anterior spines) % (protaspis width)	55/75	95/55	95/110	75/80
(length of ventral aperture) % (length of protaspis)	65	60	60	60
sculpture	smooth	smooth	smooth	pitted
<b>MERASPIS CEPHALON</b>				
range in length (mm)	1.4/2.0	-/2.2	1.1/3.1	1.5/4.5
(width across palpebral lobe) % (length of cranidium)	85/90	95/90	115/90	-/95
(maximum preocular width) % (palpebral width)	85/95	80/100	75/85	-/75
(basal width of glabella) % (preocular width)	65/70	60/70	45/65	45/70
(length of anterior extremity of palpebral lobe from front of glabella) % (length of glabella)	45/50	-/50	40/50	50/50
preglabellar ridge	strong	slight	strong	moderate
slope of palpebral lobe	moderate	slight	strong	moderate
(length of genal spine) % (estimated cephalic length)	55/45	47/50	45/-	-
(length of median suture) % (estimated length of cephalon)	35/-	-/35	30/-	30/-
<b>HYPOSTOME</b>				
(sagittal length) % (exsagittal length)	60	55	75	65
<b>TRANSITORY PYGIDIUM</b>				
(sagittal length) % (width)	60/60	65/80	60	5
(anterior width of axis) % (maximum width of pygidium)	30/40	30/-	30/35	25/-
sagittal length to which posteromedian notch retained	1.6	1.8	1.9	?
sculpture	smooth	smooth	smooth	pitted

*Isotelus* sp. B

Plate 54, figs. 3 and 4; Plate 56, figs. 1-8; Plate 57, fig. 9; text-fig. 5D

*Material.* See Plate explanations for specimen details. Loc. 1A, upper Lincolnshire Formation, Middle Ordovician.*Description.* Differs from *I. giselae* as follows: largest cranidium (text-fig. 5D), 29 mm in sagittal length, minimum width 80 % sagittal length, situated posterior to midlength of cranidium; surface finely pitted; hypostome with broader apex to notch and reduced posterior wings. Protaspides differ in their shorter marginal spines, and much more broadly rounded and swollen posterior area. Meraspis cranidia differ in the



broader glabella and stronger convexity; palpebral lobe somewhat elevated in a late meraspis cranidium, BMNH It 17291 (Pl. 56, fig. 2). Shoulder spine of meraspis hypostome further forward; transitory pygidium more weakly segmented.

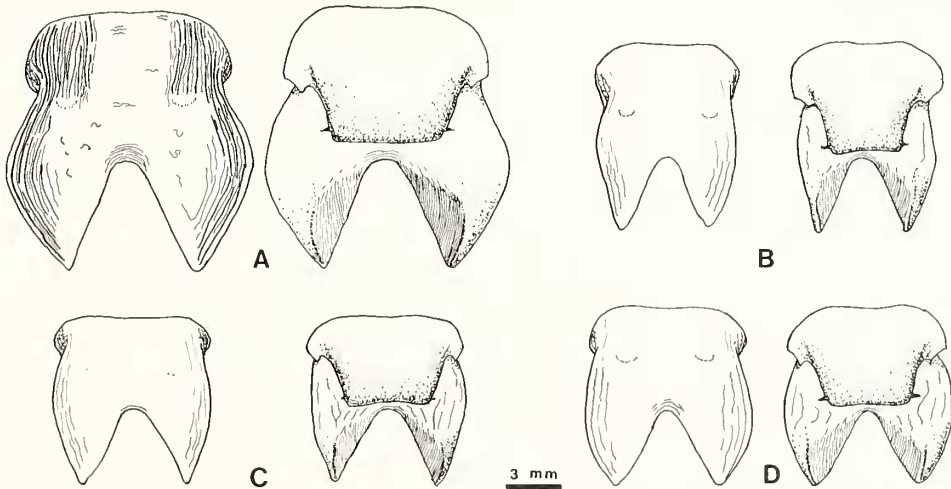
*Discussion.* The adult cranidium closely resembles *I. giselae* (text-fig. 5A-C) but the course of the anterior branch of the facial suture is less angular. There is a great difference between the protaspides of the two species, and meraspis parts are readily distinguishable (Table 3).

*Isotelus* sp. C

Text-fig. 6B

*Material.* Loc. 8, Oranda Formation, Middle Ordovician.

*Discussion.* Adult hypostomes are the only parts sufficiently well preserved for comparison, and they establish the distinctness of this species (text-fig. 6); they differ from those of the other species described in being more elongate, width 75 % length (exsag.); the posteromedian notch is 40 % the length (exsag.) of the hypostome, and the tips of the forks are 60 % the maximum width of the hypostome apart. Protaspides and meraspides are poorly preserved.



TEXT-FIG. 6. Reconstructions of adult *Isotelus* hypostomes (left, ventral view; right, dorsal view). A, *I. giselae* sp. nov., Edinburg Formation. B, *I.* sp. C, Oranda Formation. C, *I.* sp. D, Martinsburg Formation. D, *I.* sp. E, Martinsburg Formation.

*Isotelus* sp. D

Plate 57, figs. 1-8, 14; text-fig. 6C

1961 asaphid indet., Evitt, pl. 117, figs. 17, 18, 22, 23.

*Material.* See Plate explanation for specimen details. Loc. 10a (Evitt 1961, p. 987), Martinsburg Formation, Middle Ordovician.

*Description.* As in the Oranda material, the only adult part adequately preserved for comparison is the hypostome, which differs from that of *I. giselae* in its less convex lateral outline, smaller anterior and posterior wings, and light sculpture. Late protaspides 0.9 mm long (sag.) illustrated by Evitt (1961, p. 117, figs. 17 and 18) differ from other species in the long axial furrows and the traces of pygidial segmentation. Furthermore,

the spines are extremely short. Small meraspis cranidia differ from *I. giselae* in the presence of the anteromedian ridge; they resemble *I. sp. A* in this respect, though the ridge is fainter.

*Discussion.* This species most closely resembles *I. sp. A* in the narrow early meraspis glabella and the anteromedian ridge. It is possible that the material described by Whittington (1941, p. 512, pl. 75, figs. 27-45, 47) is conspecific but the axis of the transitory pygidium is less strongly defined posteriorly, and the anterior margin of the hypostomal doublure is transverse, not bowed forwards, in *I. giselae*. As Evitt (1961, p. 988) has mentioned, the only other genera of trilobites occurring at this locality are a calymenid and a cheirurid, leaving *Isotelus* as the only candidate for the protaspides assigned to it.

*Isotelus sp. E*

Plate 54, figs. 7, 8, 18-20; text-fig. 6D

*Material.* See Plate explanation for specimen details. Loc. 9, 10, 11, 12, and 2 of Evitt (1953, p. 34).

*Description.* Adult hypostomes differ from those of *I. sp. D* in the larger anterior and posterior wings, and in the stronger keel on the doublure of the posterior fork. Early protaspides differ from other species described in being more triangular and strongly pitted, a sculpture which is retained in some degree throughout development. The late protaspis is broadly rounded posteriorly, the glabella is much shorter than in the foregoing Martinsburg Formation species, and there is no trace of segmentation. Protaspis hypostomes agreeing with Stages 2, 3, and 4 of the Edinburg Formation material occur; the late stages differ in the deeper doublure, giving the lateral spines a gun-turret appearance (Pl. 54, fig. 20). Meraspis parts of this species are not clearly distinguishable from the foregoing species.

Genus NAHANNIA Chatterton and Ludvigsen, 1976

*Type species.* *Nahannia humilisulcata* Chatterton and Ludvigsen, 1976, Esbataottine Formation, District of Mackenzie, Canada.

*Nahannia sp.*

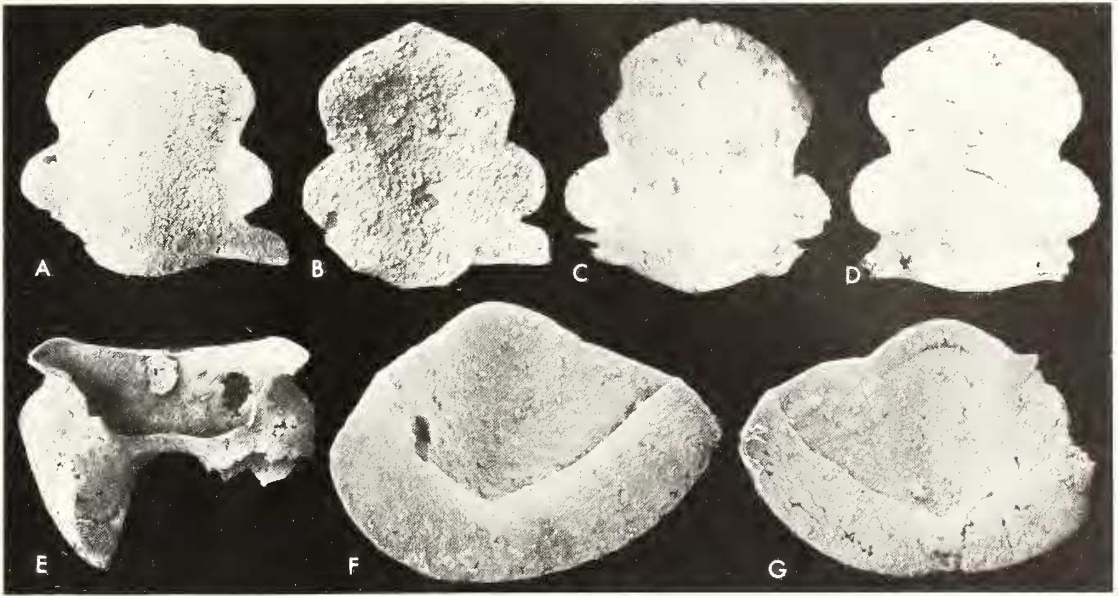
Plate 55, figs. 33-35; text-fig. 7

*Material.* See Plate and text-figure explanations for specimen details. Loc. 1, lower Lincolnshire Formation. Loc. 1a, upper Lincolnshire Formation, Middle Ordovician.

*Description.* Cranidia 1.5-3.8 mm long with glabella and occipital ring faintly and decreasingly defined, narrowing opposite anterior extremity of palpebral lobe. Minimum width 60-70 % sagittal length, and 80-90 % preocular width, situated opposite midlength of cranium. Palpebral lobe 30 % length of cranium, horizontal. Anterior branches of facial suture diverge to 85 % palpebral width, thence curving to midline. Posterior branch curves backwards and outwards, cutting posterior margin at a steep angle.

Hypostome BMNH It 19063 (text-fig. 7E), the largest part found, 6.8 mm long (exsag.), 75 % long as wide, weakly convex. Anterior margin gently concave forwards, curving downwards and backwards at anterior wing. Lateral margin indented posterior to wing, strongly rounded in outline anteriorly, weakly so for most of length. Middle body undefined. Macula eroded, situated opposite lateral indentation at about midwidth of hypostome. Inner margin of fork curved gently inwards. Doublure extends forward from fork to anterior wing laterally. Anterior margin transverse for less than half width of hypostome anterior to median embayment, curving obliquely and sinuously forwards and outwards to anterior wing. Longitudinal keel on fork curves sigmoidally forwards from tip, dying out anteriorly; inner slope flat, bevelled, bearing faint, closely spaced, straight, parallel raised lines slanting forwards and inwards.

Transitory pygidia incorporating one thoracic segment (Pl. 55, figs. 33 and 34; text-fig. 7G) 1.9-2.5 mm long, as long as wide; inner area with gentle independent convexity, outer area slightly concave. Axis bowed forwards for 45 % anterior width, narrowing steadily to apex at 70 % length of pygidium from front, indistinctly defined by stronger convexity. Posterior margin broadly rounded. Articulating half ring not seen. Articulating facet distinct but small. Doublure 30 % length (sag.) of pygidium, anterior margin slightly embayed for 5 % width; terrace lines closely spaced, faint, gently convergent. Small holaspis pygidium BMNH It 17305 (Pl. 55, fig. 35) 2.8 mm long, 60 % as long as wide, axis 40 % maximum width, defined anteriorly only. Inner area moderately convex, with a well-marked concave depression setting off a weakly convex abaxial area. Doublure



TEXT-FIG. 7. *Nahannia* sp. A-F, upper Lincolnshire Formation, loc. 1a. A-D, meraspis cranidia; A, It 17288,  $\times 25$ ; B, It 19056,  $\times 20$ ; C, It 19057,  $\times 18$ ; D, It 17290,  $\times 10$ . E, It 19063, hypostome, ventral view,  $\times 4.5$ . F, It 17305, small pygidium, ventral view (dorsal view, Pl. 55, fig. 35),  $\times 13$ . G, lower Lincolnshire Formation, loc. 1; It 17277, transitory pygidium, ventral view (dorsal view, Pl. 55, fig. 33),  $\times 16$ . All BMNH specimens.

25 % length (sag.) of pygidium, anterior margin slightly embayed mesially; terrace lines faint, oblique. Dorsal surface smooth externally.

**Discussion.** The adult hypostome described above differs from *Isotelus* and corresponds with *Nahannia* in being relatively wider, and in the deeper posteromedian embayment, which exceeds 50 % of the sagittal length of the pygidium. It differs from the hypostome of the type species, *N. humilisulcata* Chatterton and Ludvigsen (1976, p. 25, pl. 3, figs. 26-29, 32, 33, 36, 37) from the Chazyan part of the Esbataottine Formation, in its greater width, and in the tips of the forks being closer together. The meraspis cranidia resemble *N. humilisulcata* and differ from *Isotelus* in the wide glabella and long palpebral lobes; the distinctive feature of adult *Nahannia* cranidia, that the preocular width exceeds the maximum palpebral width, is not evident in the meraspis. Lincolnshire Formation juvenile cranidia differ from *N. humilisulcata* in the narrower preocular width, and more forward position of the palpebral lobe; pygidia differ in their weaker convexity and absence of segmentation. Chatterton and Ludvigsen listed other occurrences of *Nahannia* in North America, ranging up to the Richmondian.

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